A cephalic sensory system with a suggested mechanoreceptive function in two pentanchine Scyliorhinidae (Elasmobranchii)

by

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ABSTRACT. - The heads of three scyliorhinid sharks (*Scyliorhinus canicula*, *Galeus melastomus*, *Apristurus aphyodes*) were investigated histologically in order to clarify the anatomy of the electroreceptive system (ampullae of Lorenzini). Complexes of ampullae of Lorenzini were digitally 3D-reconstructed according to section series and superficial pore patterns belonging to the complexes were mapped. Neurocranial structures were reconstructed with computertomography. These investigations revealed that not all pore fields on the surface of the head in *G. melastomus* and *A. aphyodes* (Pentanchinae) are part of the electroreceptive system as generally assumed: mediorostral pore fields dorsally and ventrally as well as preorbital and supralabial pore fields in both species are part of a subdermal system of shallow solitary grooves, surrounded by the same dense connective tissue as the canalicular mechanoreceptive lateral line. Histological sections show digitiform protuberances and maculae similar to neuromast organs of the epithelia in the groove system in *G. melastomus*. Accordingly, histology rather indicates a mechanoreceptive function. The exact function or biological role and the phylogenetic significance of this elaborate system in two pentanchine catsharks are by no means clear yet. A similar groove system was found in *A. fedorovi, A. herklotsi* and *G. murinus*. In *S. canicula* (Scyliorhininae) no comparable grooves or pores are found.

RÉSUMÉ. - Un système sensoriel céphalique avec une possible fonction mécanoréceptive chez deux Scyliorhinidae pentanchines (Elasmobranchii).

Les têtes de trois requins de la famille des Scyliorhinidae (*Scyliorhinus canicula, Galeus melastomus* et *Apristurus aphyodes*) ont été étudiées en histologie dans le but de clarifier l'anatomie du système électroréceptif (ampoules de Lorenzini). Les complexes de Lorenzini ont été reconstruits en 3D sur la base des séries de sections et les schémas des pores superficiels appartenant aux complexes ont été établis. Les structures neurocraniennes ont été reconstruites par tomographie assistée par ordinateur. Les investigations ont révélé que tous les pores à la surface de la tête de *G. melastomus* et d'*A. aphyodes* (Pentanchinae) n'appartiennent pas au système électroréceptif. Les pores médiorostraux des faces dorsale et ventrale ainsi que les pores préorbitaux et supralabiaux chez les deux espèces font partie d'un système sous-cutané constitué de cavités isolées, entourées par un tissu conjonctif dense identique à celui de la ligne latérale mécano-réceptive. Les sections histologiques montrent des protubérances digitiformes et des maculas semblables aux neuromastes de l'épithélium dans le système cavitaire de *G. melastomus*. En conséquence, l'histologie suggère une fonction mécano-réceptive. Toutefois, des incertitudes persistent concernant la fonction exacte ou le rôle biologique et la signification phylogénétique de ce système complexe chez les deux Pentanchinae étudiés. A noter qu'un système cavitaire similaire existe chez *A. fedorovi*, *A. herklotsi* et *G. murinus*, mais pas chez *S. canicula* (Scyliorhininae).

Key words. - Scyliorhinidae - Pentanchinae - *Apristurus* - *Galeus* - Cranial pore fields - Lateral line - Morphology - Histology.

As known to date, apart from the sense of vision, smell and gustation, all chondrichthyans possess at least two major cranial sensory systems: The cephalic mechanoreceptive lateral line system and the electroreceptive system of ampullae of Lorenzini. Both systems develop from dorsolateral placodes, embryonic neuroectoderm in the widest sense, and development sites are closely adjacent, but show wide differences in ontogenesis, morphology and function (e.g., Ewart, 1892; Ewart and Mitchell, 1892; Holmgren, 1942; Disler, 1961; Fishelson and Baranes, 1998a; Gibbs and Northcutt, 2004). The investigation of the ampullae of Lorenzini has a long history (e.g., Ewart, 1892, Ewart and Mitchell, 1892; Allis, 1901; Metcalf, 1915; Allis, 1923; Dotterweich, 1932; Dijkgraaf and Kalmijn, 1963; Kalmijn, 1966; Murray, 1974; Raschi, 1978, 1986; Raschi *et al*., 2002; Collin and Whitehead, 2004), but only few studies attempt to systematically describe the complex arrangement of the tripartite ampullary system (ampullary sac, tubuli, pore fields) (Chu and Meng, 1979; Fishelson and Baranes, 1998b). Most of the literature is fragmentary, describing separate elements of the total electroreceptive system (Raschi and Mackanos, 1987).

The superficially visible pore series and pore fields on the head of a shark are normally accepted as lateral line pores and openings of Lorenzinian ampullae, respectively. The mechanoreceptive lateral line is organised into canalicular

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pores and some distinct grooves of pit lines of free neuromast organs which both form patterns that are characteristic of major vertebrate clades (e.g., Holmgren, 1942; Tester and Nelson, 1969; Peach and Rouse, 2000). For *Galeus melastomus* (Atkinson and Bottaro, 2006) and the genus *Apristurus* (Nakaya and Sato, 1999) so far nothing unusual is described. The inner organisation of superficially identical cephalic pore fields, however, might differ in different species as observed in our comparative study of three scyliorhinid sharks, *Galeus melastomus* Rafinesque, 1810, *Apristurus aphyodes* Nakaya & Stehmann, 1998 and *Scyliorhinus canicula* (Linnaeus, 1758). In addition, we also found pore fields dorsally and ventrally on the head in *G. melastomus* and *A. aphyodes* which are formed by structures completely different from ampullae of Lorenzini and so far macro- and microscopically described elasmobranch lateral line organs (Garman, 1888; Tester and Nelson, 1969; Barry *et al*., 1988; Barry and Bennett, 1989; Maruska and Tricas, 1998; Peach, 2003; Maruska, 2001). Further investigations of other species of the genera *Apristurus* and *Galeus* revealed that all examined representatives of Pentanchinae possess these pore fields. As far as we know this is the first description of such structures in Elasmobranchs.

MATERIALS AND METHODS

A male juvenile specimen of *Galeus melastomus* (total length 165 mm, head length 25 mm) was collected in 1996 by Peter Bartsch in the Western Mediterranean near Palamos, Catalunya, Spain (trawl, max. depth 500 m), fixated in 4% formalin and stored in 70% ethanol. A male juvenile *Apristurus herklotsi* (Fowler, 1934) – ex MUFS 22894, 213.9 mm TL, off Dashi (Tashi), northeastern Taiwan, below 1000 m depth, 18 May, 2005 was provided by Profs. Yukio Iwatsuki and Kazuhiro Nakaya. The head embedding for Light Microscopy was conducted with paraffin using a Hypercenter XP embedding automat. The paraffin block was cut with a Leica SM2000 R using disposable Feather S 35 blades (thickness 12 µm). Staining followed with Heidenhain's Azan. The adult specimen (male) of *A. aphyodes* (total length 536 mm, head length 100.5 mm) coll. 2002 in the North Atlantic Ocean (max. depth 2000 m), fixated in 4% formalin and stored in 70% ethanol. It was provided by Drs. Samuel Iglésias and Daniel Sellos, Concarneau, France. The head was embedded in celloidine and cut in sections of 100 µm using a Leica sledge microtome SM2500 M, and reusable Leica blades (300 mm) with A-cut. The sections were stained with Weigert haematoxyline and eosine (HE) because tests with Heidenhain's Azan delivered unsatisfactory results. Celloidine is difficult to handle, highly time-consuming and applications sometimes fail. Therefore celloidine was used for *A. aphyodes* only, which was too big for paraffin embedding.

The selected histological sections of the head of *A. aphyodes* and *G. melastomus* (250 of *A. aphyodes*, 150 of *G. melastomus*) were digitized with a Progress 3012 mF camera connected to an INTEQ computer using analySIS 3.1. For reconstruction the photos were loaded in the 3D-module of analySIS 3.1 on a DELL Dimension 4500 computer.

For more detailed topographical relationships, reconstructions of the endocrania in *A. aphyodes*, *G. melastomus*, *Scyliorhinus canicula*, and *Galeorhinus galeus* were done with computertomography at the Radiological Department of the Virchow Klinikum of the Charité in Berlin.

For *Galeorhinus galeus*, *S. canicula* and *A. aphyodes* a GE Light Speed 16 computertomograph was used with a connected HP 8000 workstation equipped with GE software AW (Advantage Workstation) 4.2 for reconstructions. Both scans were conducted with 120 kV, 280 mA and a resolution of 0.6 mm. *G. melastomus* was scanned with a new GE Light Speed VCT connected to the workstation described above. The scan was conducted with 100 kV, 145 mA and a resolution of 0.6 mm.

Several specimens were used for macroscopical dissections and comparison:

G. melastomus Rafinesque, 1810 – four heads of adult individuals from Mediterranean and North Atlantic (coll. by Drs. Sven Gemballa and Samuel Iglésias, respectively); *A. fedorovi* Dolganov, 1985 – one female (TL 430 mm, head length 83 mm), Japan 2002, 1500 m maximum depth; *A. aphyodes* Nakaya & Stehmann, 1998 – one female (head length 100.3 mm) Northern Atlantic, 2000 m maximum depth (coll. Samuel Iglésias); *Scyliorhinus canicula* – several specimens from Northern Atlantic; *G. murinus* Collet, 1904 – one juvenile specimen, head length 55 mm (coll. Daniel Sellos and Samuel Iglésias, Concarneau). *Mustelus asterias* Cloquet, 1821 – one specimen, head length 95 mm was collected at the 290th field trip of the Walther Herwig II (Bundesforschungsanstalt Hamburg) in the North Sea.

Controls of lateral line canal distribution and interconnections were performed by ink or methylene-blue injections. The terminology of the lateral line canal system largely follows the detailed nomenclature of Garman (1888).

RESULTS

The electroreceptive system in *A. aphyodes*, *G. melastomus* and *S. canicula* was investigated thoroughly. Here we give just a brief outline of how the ampullae of Lorenzini organise: The ampullary sacs which contain the receptive epithelia within their alveoli lie in clusters in distinct areas of the head. All ampullae extend, in some cases of our medium-sized specimens up to approximately 80 mm long, jelly-filled tubuli. The tubuli of one ampullary cluster extend in

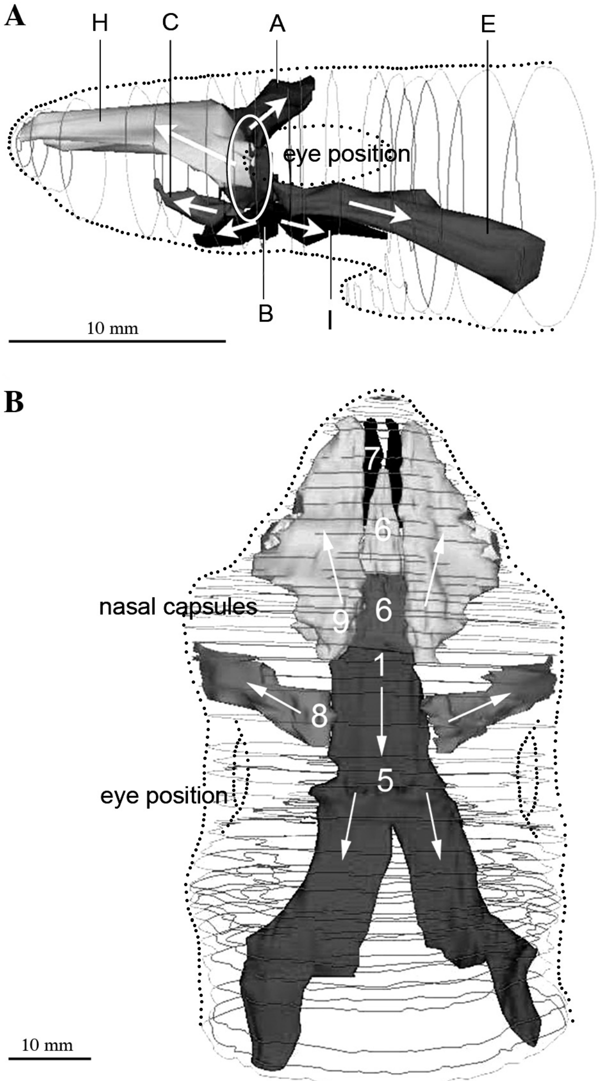

Figure 1. - Computed 3-D reconstructions from histological serial sections. Extension and arrangement of complexes of Lorenzinian ampullae in two pentanchine catsharks. **A**: *Galeus melastomus*, lateral view on all complexes innervated by the ramus buccalis (buccal complexes). **B**: *Apristurus aphyodes*, dorsal view on complexes innervated by the ramus ophthalmicus superficialis (ophthalmic complexes). Arrows point into the direction of tubule extension. Numbers and letters provisionally name the different complexes. Cross-sections is indicated by thin lines. The ellipse in **A** encircles the ampullary clusters forming the buccal aggregation. *[Reconstruction 3-D informatique à partir d'une série histologique. Disposition des complexes d'ampoules de Lorenzini chez deux Pentanchinae.* ***A:*** G. melastomus*, vue latérale des complexes innervés par le ramus buccalis.* ***B:*** A. aphyodes*, vue dorsale des complexes innervés par le ramus ophthalmicus superficialis. Les flèches pointent dans la direction de l'extension des tubules. Les nombres et les lettres nomment provisoirement les différents complexes. Les plans de coupes sont indiqués par des lignes fines. L'ellipse en* ***A*** *encercle le groupement d'ampoules formant l'agrégat buccal.]*

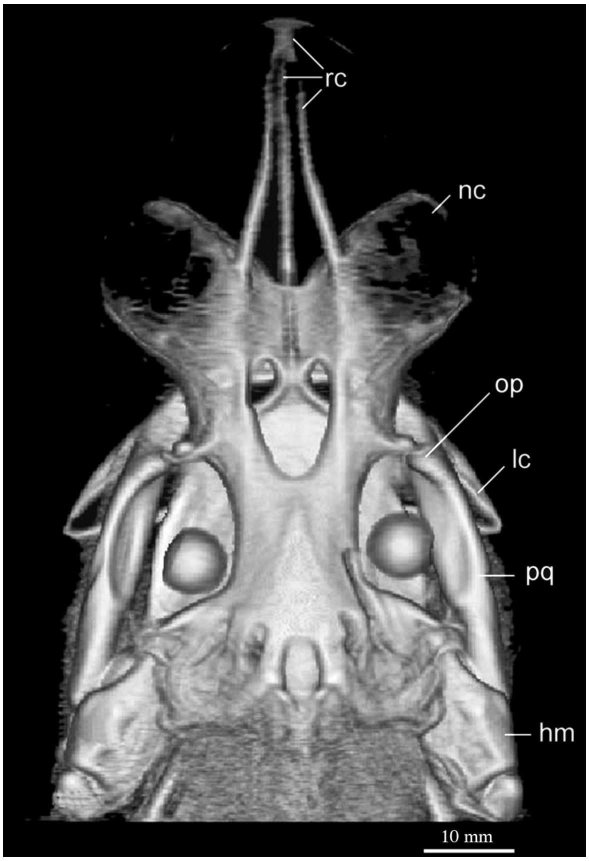

Figure 2. - Computed 3-D reconstruction of the chondrocranium of *Apristurus aphyodes* in dorsal view. hm, hyomandibula. lc, labial cartilage. nc, nasal capsule. op, orbital process (of palatoquadrate). pq, palatoquadrate. rc, rostral cartilages (observe the faint subcutaneous extension of connective tissue at the rostral tip accommodating the rostral and subrostral lateral lines). 120 kV, 280 mA, 0.6 mm resolution, 2-fold. *[Reconstruction 3-D informatique du chondrocrâne d'*A. aphyodes *en vue dorsale.]*

the same direction and form a common pore field on the skin. One ampullary cluster with its tubuli and the corresponding pore field was named complex. Each complex was digitally reconstructed as we followed the tubuli from the ampullary sacs to the pore fields in the serial sections (Fig. 1). The ampullary clusters are deeply embedded in the head, the voluminous complexes in *Galeus* and *Apristurus* accommodated by spaces of the neurocranium (Fig. 2). The reconstructions of the complexes with their corresponding pore fields demonstrably left out certain pore fields on the head in *G. melastomus* and *A. aphyodes*. These pore fields are not connected to the electroreceptive system at any point. In the following we will describe the morphology of the structures which form these pore fields.

Special pore fields

The pore fields in question are the most prominent ones on the head in the investigated species of *Galeus* and *Apristurus* and are located as follows: Most eye-catching are leave-like oval mediorostral pore fields dorsally and ventrally. On the dorsal side the pore field is paired and completely separated over the midline. It extends from the nasal cap-

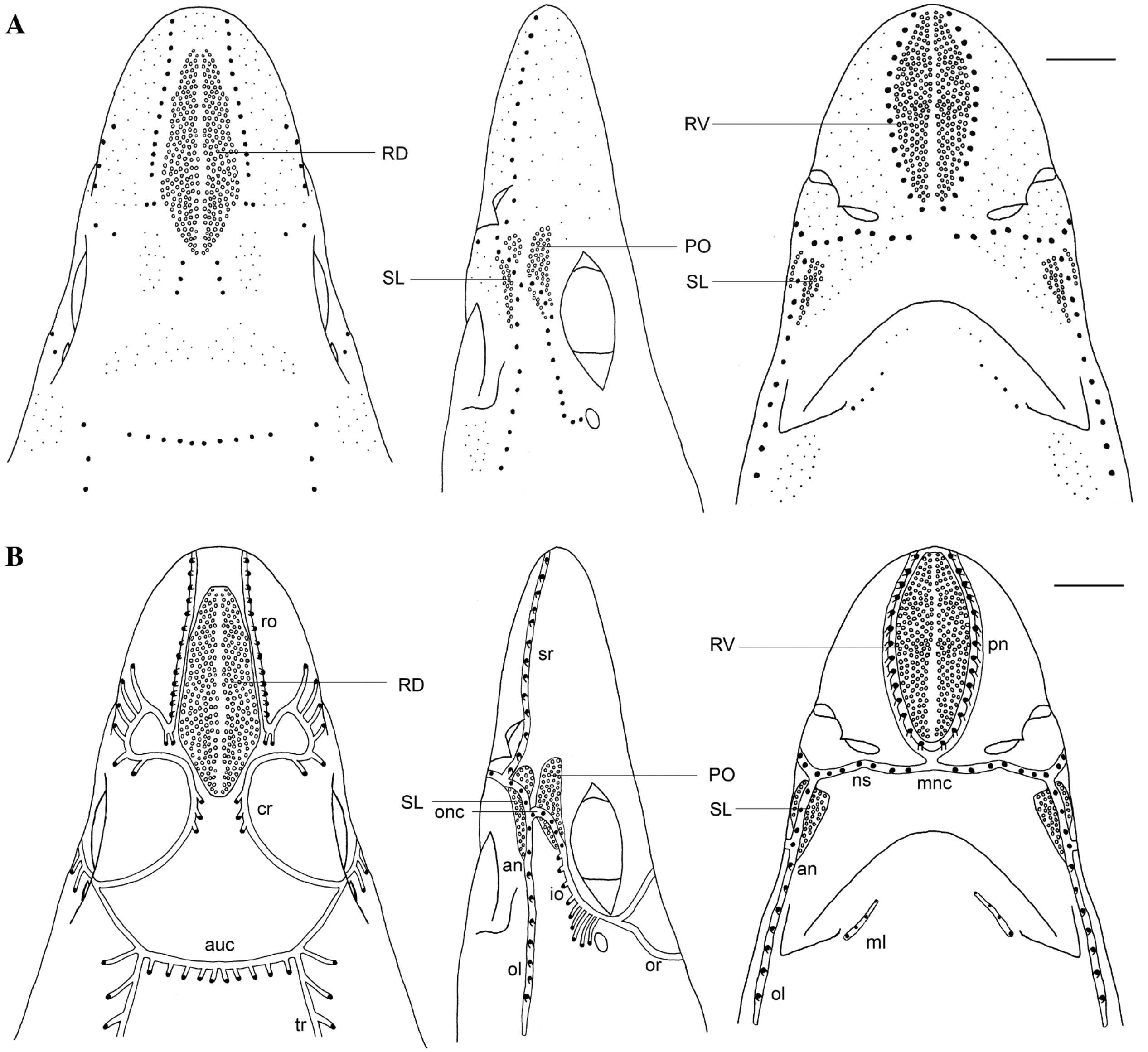

Figure 3. - **A**: Survey of all pore fields found on the head surface of *Galeus melastomus*. From left to right: Dorsal, lateral and ventral view. Open dots: Pores of the groove system. Small dots: Pore of the ampullae of Lorenzini. Full dots: Lateral line pores. Pore fields of the groove system: PO, preorbital. RD, rostrodorsal. RV, rostroventral. SL, supralabial. **B**: Cephalic lateral line canals in *G. melastomus* together with the groove patches. Groove patches: PO, preorbital. RD, rostrodorsal. RV, rostroventral. SL, supralabial. Supraorbital lateral line canals: auc, aural (temporal) commissure. cr, cranial line. or, orbital line. ro, rostral line. tr, trunk line. Suborbital lateral line canals: an, angular line. io, infraorbital line. ml, mandibular line. mnc, median nasal commissure. ns, nasal line. ol, oral line. onc, orbitonasal commissure. pn, prenasal line. sr, subrostral line. Scale bars = 10 mm. *[**A**: Relevé des champs de pores trouvés à la surface de la tête de* G. melastomus.*]*

sules cranially over the rostrum and ends a little behind the tip of the rostrum [Figs 3A, 4A (RD, rostrodorsal pore field)]. On the ventral side a corresponding pore field shows a separation only in the posteriormost part and extends from the caudal end of the nasal apertures right to the tip of the rostrum [Figs 3A, 4A (RV, rostroventral pore field)]. On each side of the head additional two pore fields are situated, one preorbitally [Figs 3A, 4A (PO, preorbital pore field)] and the other one on the ventral side between the nasal apertures and the upper jaw [Figs 3A, 4A (SL, supralabial pore field)]. *Apristurus* and *Galeus* show a general difference in head shape: The head of *Apristurus* in most species of this genus is rather flat with a spatulate rostrum and only presents a wide dorsal and ventral area without an extended cheek and preorbital region. In contrast, *Galeus* clearly has a more robust head with a voluminous rostrum. Therefore the homologous preorbital pore fields are laterally positioned in *Galeus* and clearly dorsally in *Apristurus*.

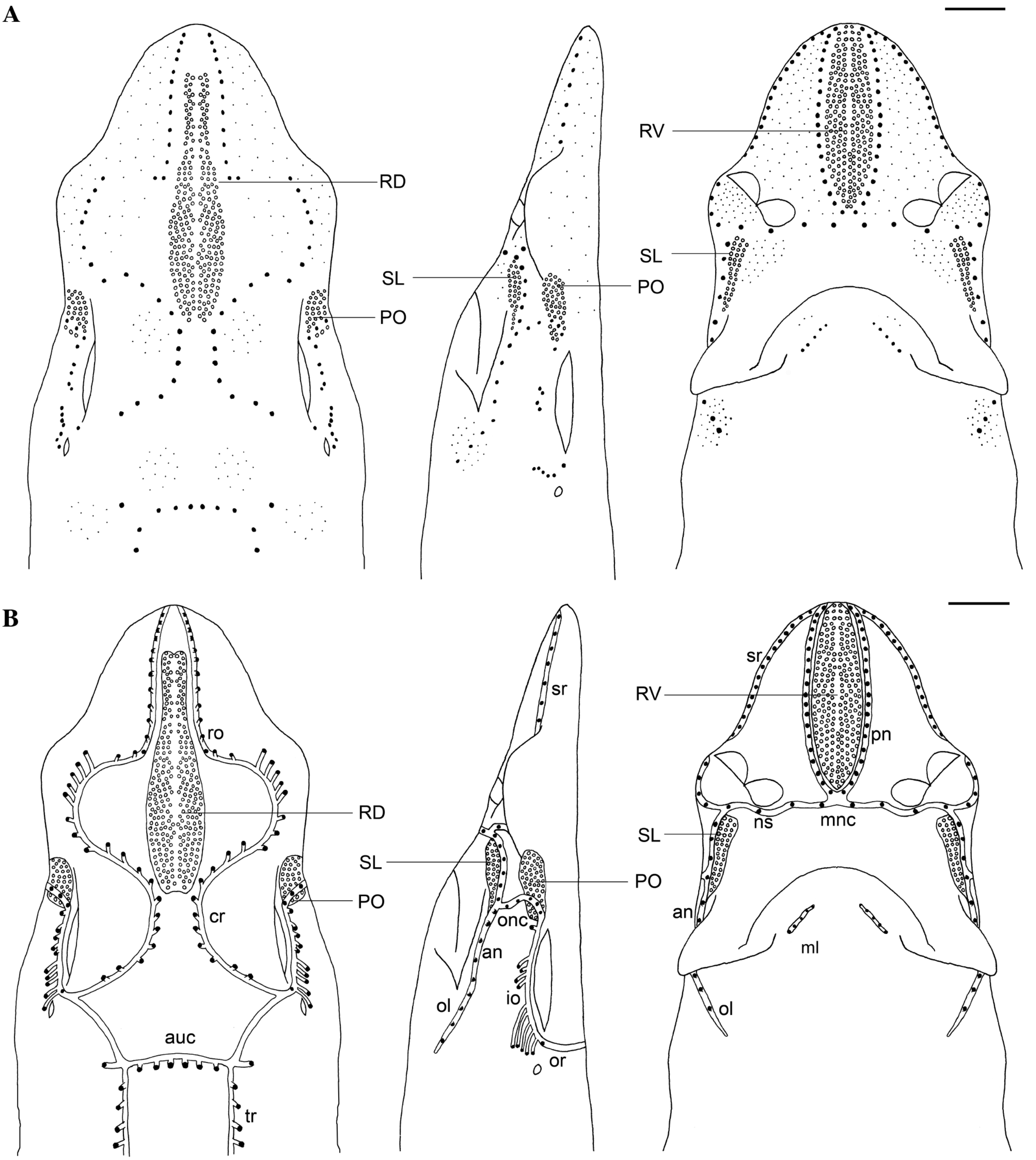

Figure 4. - **A**: Survey of all pore fields on the head of *Apristurus aphyodes*. From left to right: Dorsal, lateral and ventral view. See Fig. 3 for captions. **B**: Cephalic lateral line canals in *A. aphyodes* together with the groove patches. *[****A****: Relevé des champs de pores trouvés sur la tête d'*A. aphyodes. ***B****: Canaux de la ligne latérale et zones cavitaires chez* A. aphyodes.*]*

Groove patches

All these pore fields in *Galeus* and *Apristurus* are contained in flat, plate-like subdermal structures of dense fibrous connective tissue (Fig. 5A). These patches show deep grooves caudally and short tubes in the rostral region. Each groove or tube stays solitary, they are not interconnected (Fig. 5B).

In *Galeus* each of the paired rostrodorsal patches is con-

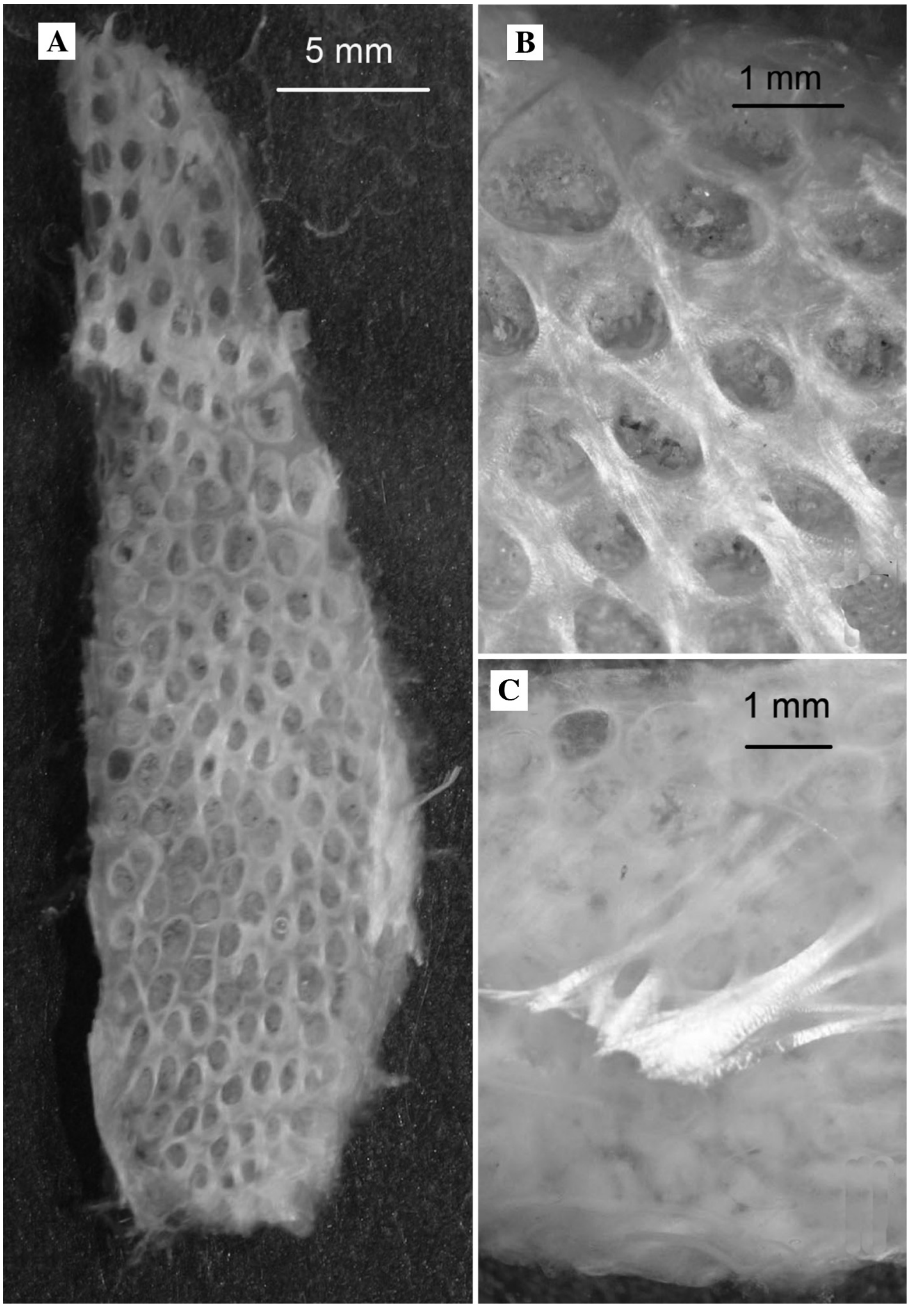

Figure 5. - Extracted right rostrodorsal connective tissue plate ("groove patch") of *Galeus melastomus*. **A**: Complete right dorsal groove patch. **B**: Close-up of the solitary grooves. **C**: Ligamentous structure on ventral side for attachment to nasal capsule. *[Couche de tissu de connexion extraite ("système cavitaire") de* G. melastomus*.* ***A*** *: Système cavitaire droit complet.* ***B*** *: Détail des cavités isolées.* ***C*** *: Face ventrale d'une structure ligamenteuse de maintien des capsules nasales.]*

nected to the nasal capsules (Fig. 2) on its side with a distinct ligament (Fig. 5C). Such ligamentous attachments are found in *Apristurus* as well but are much less distinct. After cutting the ligamentous bands, the patches in the dorsal region of the head are easily removed from the surrounding tissues; they are purely superficial structures (Figs 6, 7). The rostroventral patch is tightly apposed to the medial rostral cartilage in *Apristurus* and *Galeus* but does not show this distinct ligamentous attachment to the cartilage. The fibrous attachments of the groove patches at the same time merge into the more general fibrous connective tissue that separates the rostral ampullae of Lorenzini into different clusters.

Groove patches and lateral line system

In *Galeus* and *Apristurus* the rostral (ro) and cranial (sphenoidal) (cr) parts of the supraorbital lateral line canals (Figs 3B, 4B) encircle the rostrodorsal groove patch. The dorsal groove patches in these genera are independent structures and there is no direct canalicular connection to the surrounding canals, which explains why tracing the groove system by injection of the lateral line fails.

On the ventral side the prenasal lines (pn) of the subor-

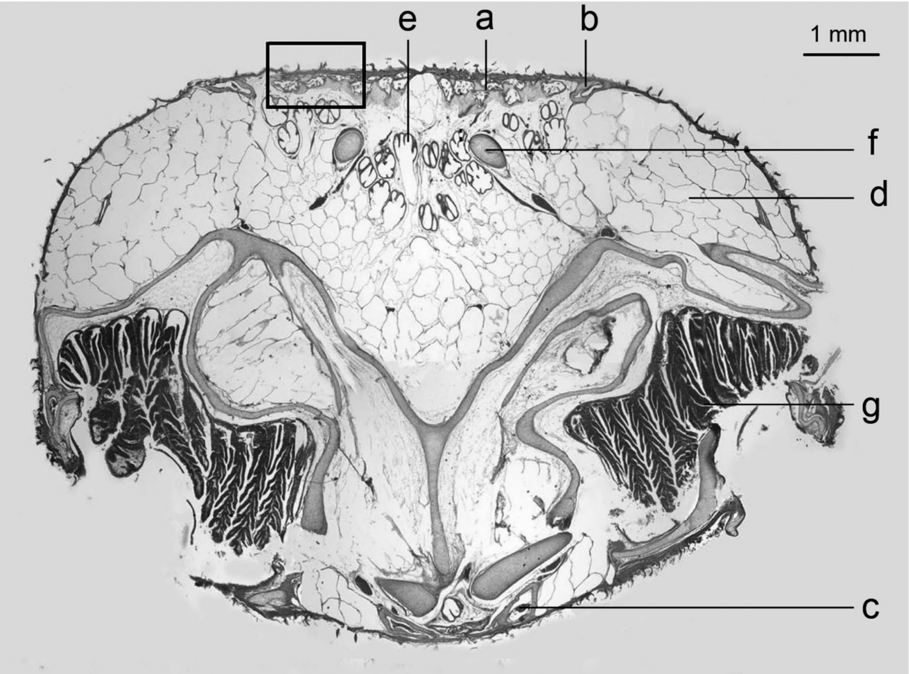

Figure 6. - Histological section through the ethmoidal region of *Galeus melastomus* at the level of the nasal openings. The rostrodorsal groove patches are well visible. These extend between the two supraorbital lateral line canals and cover the ampullary sacs of the ophthalmic aggregation. Frame enlarged in Fig. 7. a, rostrodorsal groove patch, left part. b, rostral section of supraorbital lateral line canal. c, prenasal section of suborbital lateral line canal. d, thick bundle of Lorenzinian tubuli in cross section. e, ampullary sacs with alveoli of Lorenzinian ampullae. f, dorsal rostral cartilage. g, aperture of nasal capsule and olfactory epithelia. *[Section histologique au travers de la région ethmoidale de* G. melastomus *au niveau des ouvertures nasales. Les zones cavitaires sont bien visibles. Elles s'étendent entre les deux lignes des canaux latéraux supraorbitaires et couvrent les sacs d'ampoules de Lorenzini de l'agrégat ophtalmique. Cadre agrandi en Fig. 7.]*

bital lateral line canals (Figs 3B, 4B) form a U-shape and surround the rostroventral groove patch closely. The rostroventral groove patch shows no clear separation of the plate of connective tissue in the midline except for the posteriormost part and some indistinct paired arrangement of grooves and pores separated along the midline. The rostroventral groove patch and the median nasal commissure (mnc) of the suborbital lateral line are tightly connected through connective tissue. Nevertheless, no direct canalicular connection is traced here as well (Fig. 8).

A very intimate relation exists between the preorbital and supralabial groove patches and the lateral line canals of the suborbital lateral line in the orbital region (io, ns, onc). The supralabial groove patch lies between nasal aperture and upper jaw. The nasal part (ns) of the suborbital lateral line sets off the subrostral line (sr) caudally of the nasal apertures and then enters the supralabial groove patch in the front. The infraorbital line part (io) of the suborbital lateral line which runs below the eye meets the nasal line (ns) here and together they form the orbitonasal commissure (onc). This joined lateral line canal runs right into the supralabial groove patch. At the caudal side of the supralabial groove patch the canal leaves the patch as the angular line (an) to continue into the jugal or oral section (ol) posteriorly which ends caudally of the angle of the mouth and the labial cartilages. There is a short, separate mandibular line (ml) section on the lower jaws running mesially and ventrally of the small mandibular ampullary field and labial cartilage. This separate mandibular section likewise is present in *Galeus melastomus* and is also described for *Mustelus*, *Triakis* and *Scyliorhinus* as a compartment of a more complete and continuous oralo-mandibulo-jugal line of *Chlamydoselachus* and Lamnidae, for example (Garman, 1888; Allis, 1901; Allis, 1934). At the dorsal margin of the supralabial groove patch the infraorbital part (io) branches off dorsally, leaves the patch and runs into the ventral side of the preorbital groove patch. The lateral line canal forms a bend within the preorbital patch and leaves it caudally to run below the eye as the infraorbital line (io) and up to the union with the orbital line (or), temporal or aural commissure (auc), and dorsal trunk line (tr) (Figs 3B, 4B).

Histology

The histological sections of the preorbital and supralabial groove patches in *G. melastomus* show the close relation between the lateral line canals and the groove patches (Figs 8, 9). Both, lateral line canal and groove patch, are surrounded as one structure by the same type of dense fibrous connective tissue that usually surrounds the mechanoreceptive lateral line in chondrichthyans. Histologically it is easily

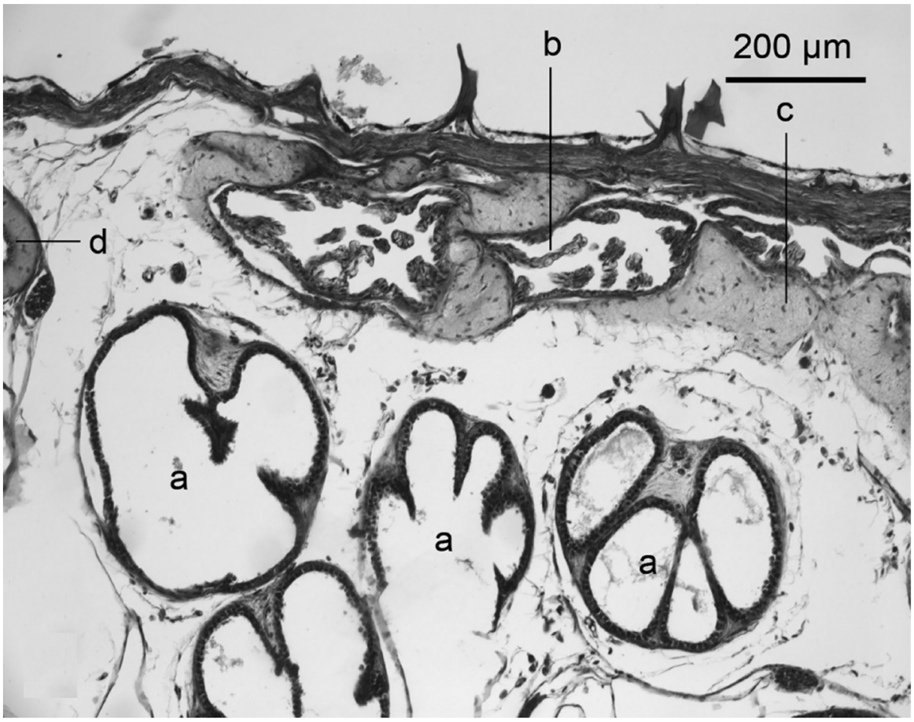

Figure 7. - Histological section through a rostrodorsal groove patch with ampullae of Lorenzini underneath in *Galeus melastomus*. Enlarged square of Fig. 6. a, ampullary sac with alveoli of ampulla of Lorenzini. b, cellular digitiform protuberance of epithelium in the groove system. c, dense fibrous connective tissue forming the groove patch. d, supraorbital lateral line canal. *[Section histologique à travers une zone cavitaire rostrodorsale au dessus d'ampoules de Lorenzini chez* G. melastomus. *Cadre de la Fig. 6.]*

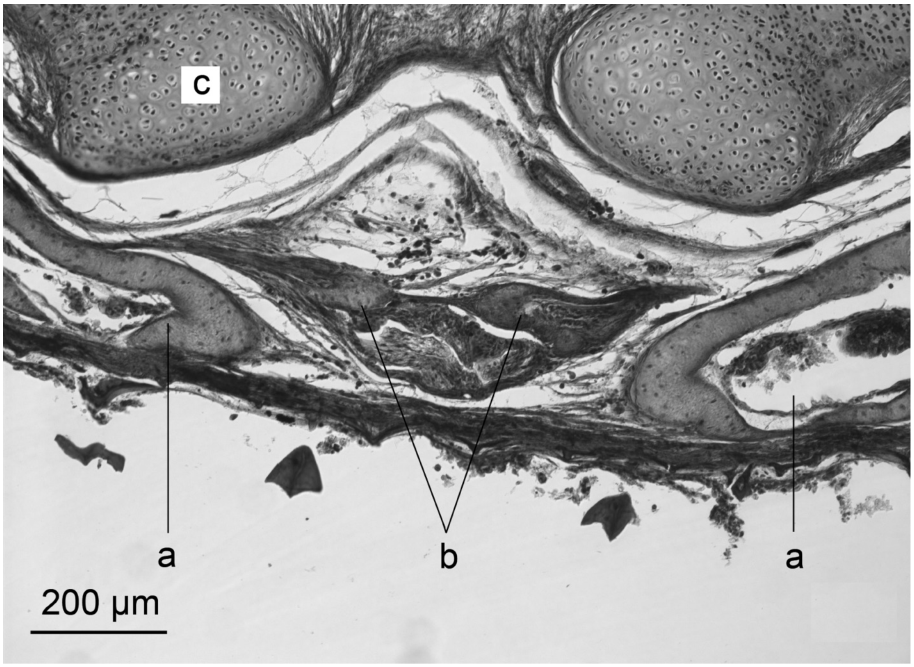

Figure 8. - Histological section of the most caudal part of the rostroventral groove patch close to the median nasal commissure in *Galeus melastomus*. There is no canalicular connection between the rostroventral groove patch and the surrounding lateral line canals. **a**, lumen and connective tissue support of the prenasal lateral line canal. b, hindmost part of rostroventral groove patch. c, ventral part of cartilaginous nasal capsules. *[Section histologique de la partie la plus caudale du système cavitaire près de la commissure nasale médiane de* G. melastomus. *Il n'y a pas de connexion canaliculaire entre le système cavitaire et les canaux périphériques de la ligne latérale.]*

confused with cartilage on a first glimpse, but contains rather fibrocyte-like cells in a densely interwoven meshwork of collagen fibres, well visible at higher magnification. Nevertheless, a direct canalicular connection between both systems cannot be traced histologically either.

The groove patches form solely plate-like superficial structures and are of completely different structure as compared to the ampullae of Lorenzini which are located around and beneath the patches (Figs 6, 7, 9). Ampullae of Lorenzini are vesicularly organised and possess always long tubuli to the body surface. The sensory epithelia in the alveoli of the ampullary sacs are invariably flat. Lorenzinian ampullae are never surrounded by the comparably thick layer of dense connective tissue as observed around all groove patches and the lateral line system (Fig. 6). None of our specimens demonstrates a filling of the grooves in the patches with jelly,

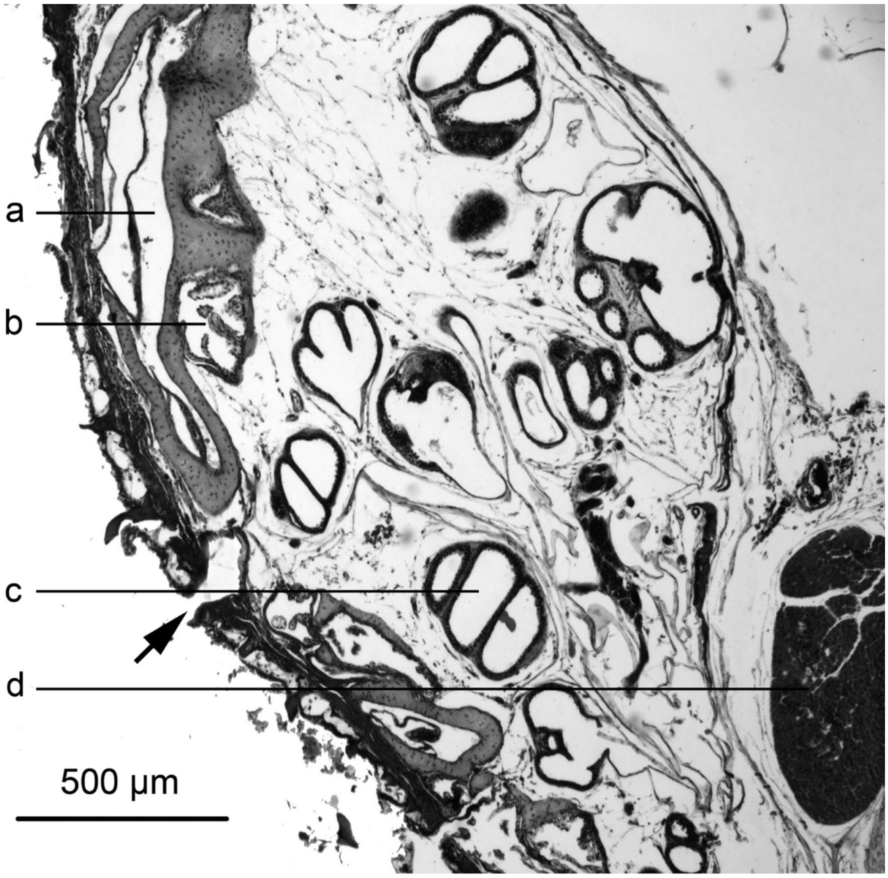

Figure 9. - Histological section through the preorbital and supralabial groove patch with the buccal aggregation of Lorenzinian ampullae proximally in *Galeus melastomus*. The infraorbital section of the suborbital lateral line canal forms a lacuna (orbitonasal commissure) within the preorbital groove patch. Lacuna and grooves underneath are contained in uniform, dense connective tissue. a, lacuna of the infraorbital lateral line canal. b, vesicle of the preorbital groove patch. c, ampullary sac of Lorenzinian ampullae within the buccal aggregation. d, ramus buccalis of Nervus facialis (VII). Arrow points to the opening of a Lorenzinian ampulla. *[Section histologique à travers le système cavitaire préorbitaire et supralabial avec agrégat d'ampoules de Lorenzini à proximité de la bouche chez* G. melastomus. *La section infraorbitaire du canal de la ligne latérale suborbitaire forme une lacune (commissure orbitonasale) au sein du système cavitaire. Les lacunes et les cavités sous-jacentes sont contenues dans un tissu conjonctif dense uniforme.]*

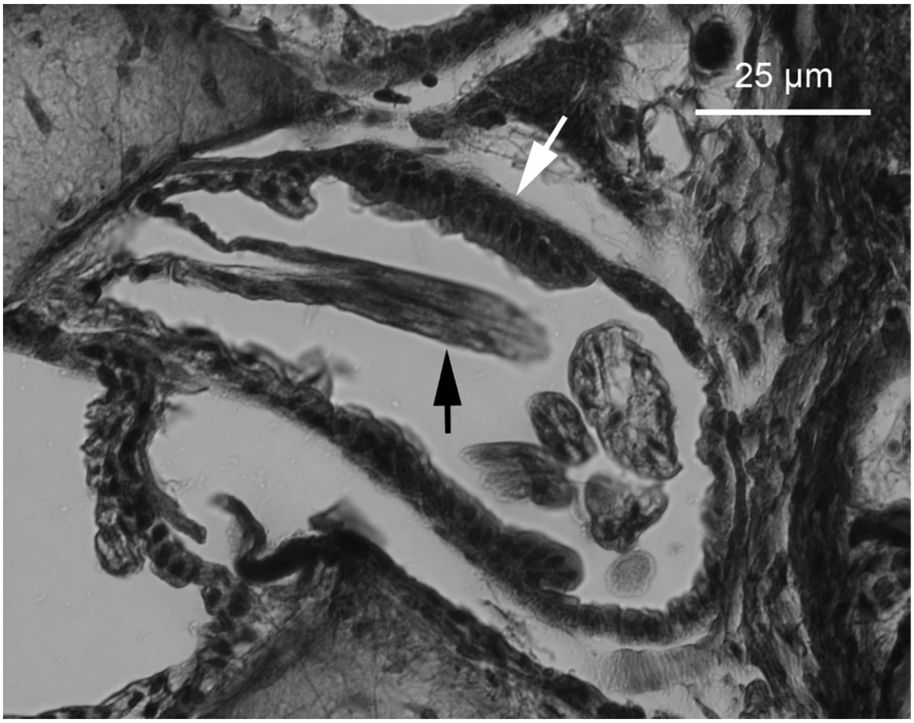

Figure 10. - Single groove of the rostroventral groove patch in *Galeus melastomus*. Black arrow, cellular digitiform protuberance. White arrow, neuromast-like macula of epithelium. *[Cavité simple du système cavitaire rostroventral chez* G. melastomus. *Flèche noire, protubérance cellulaire digitiforme. Flèche blanche, macula de l'épithélium semblable à un neuromaste.]*

which is typical for ampullae of Lorenzini.

The grooves are completely lined by an epithelium. In contrast to the flat receptive epithelia inside the ampullae of Lorenzini the epithelium in each groove shows numerous cellular digitiform protuberances (Figs 7, 10). These protuberances are of remarkable length compared to the groove diameter. Within the protuberances at the ground of the grooves macula structures were identified which resemble closely neuromast organs only found in the mechanoreceptive lateral line and stato-acoustic systems (Fig. 10).

As can be traced even macroscopically, the rostrodorsal groove patch is innervated by branches of the rami ophthalmici superficiales as are the ampullae of Lorenzini and the lateral line system in this region of the head. The ventral groove patch is supplied by the rami buccales as are the supralabial and preorbital groove patches.

DISCUSSION AND CONCLUSION

Without any question the structure of the grooves and groove patches differs considerably from the ampullae of Lorenzini as described by many authors (e.g., Dotterweich, 1932; Fishelson and Baranes, 1998a, 1998b; Raschi and Mackanos, 1987; Allis, 1923; Dijkgraaf and Kalmijn, 1963; Metcalf, 1915; Raschi, 1986; Collin and Whitehead, 2004; Raschi *et al*,. 2002) and examined in our study in *Galeus melastomus*, *Apristurus aphyodes*, and *Scyliorhinus canicula*. It is, however, by no means clear so far which function this groove system has.

The most uncommon feature of the grooves are the cellular protuberances of the inherent epithelium. As far as we know, such protuberances are neither described for electroreceptive nor mechanoreceptive structures in any fish (e.g., Garman, 1888; Ewart, 1892; Johnson, 1917; Norris, 1929; Ekström v. Lubitz, 1981; Rouse and Pickles, 1991; Cernuda-Cernuda and Garcia-Fernandez, 1996; Marshall, 1996; Maruska and Tricas, 1998; Maruska, 2001; Bensouilah *et al*., 2002; Peach, 2003; Collin and Whitehead, 2004; Gibbs, 2004). In any case, one may speculate that the protuberances could serve for compartmentalisation. The small stationary water bodies in the grooves already separated from the surroundings would be subdivided and maybe highly sensitive for current changes and their directions producing an enhanced wide-range tactile system. Considering the tight connection to the mechanoreceptive lateral line system and the histology of the receptive epithelia an electroreceptive function is highly unlikely and a mechanoreceptive function is much more probable.

Only one vague hint so far was found in the literature on the existence of these grooves in other species. Norris (1929) describes certain "glands" in the "innervation areas" of the ampullary parts of the Lorenzinian ampullae, i.e., the ophthalmic and buccal aggregations of *Cephaloscyllium ventriosum* (Scyliorhininae). Norris offers no suggestion concerning the significance of these "glands" and he failed to notice the epithelium protuberances, probably due to insufficient fixation. The epithelium decays very quickly and leaves nothing than the cartilage-like groove system.

If the investigated specimen of 1929 really was *Cephaloscyllium ventriosum*, and the "glands" of Norris are the same system, this would falsify our idea of the grooves system being a synapomorphic character, phylogenetically derived for the pentanchine catsharks *Apristurus* and *Galeus* and closely related species. This assumption is based on our simultaneous investigation of *Scyliorhinus canicula* (Scyliorhininae) devoid of such grooves. However, monophyly of the family Scyliorhinidae and sister-group relationship of Scyliorhininae and Pentanchinae is debated for good reasons as well (Iglésias *et al*., 2005). With the limited number of taxa investigated here, at present we cannot ascertain the uniqueness of this groove system among a certain carcharhiniform subgroup.

A thorough investigation of other pentanchine catsharks and further related groups among Carcharhiniformes such as Triakidae and Proscyllidae not only will establish the phylogenetic significance of the groove system but possibly provide an array of structural and evolutionary intermediates too. In *Mustelus asterias*, *Galeorhinus galeus* (Triakidae) and other triakids (Garman, 1888; Chu and Meng, 1979; Fishelson and Baranes, 1998a) for example, the lateral line canals show excessive branching with formation of lateral line pore fields in the same areas of the head where the groove patches were found in *Galeus* and *Apristurus*, a fact that might indicate that the peculiar pentanchine groove system derives from such elaborate and systematically widespread, branched lateral-line systems phylogenetically.

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